The generic status of *Oxyanthus gossweileri* (Rubiaceae) from Angola

E. Robbrecht*, S. Huysmans[1] and E. Figueiredo[2]

*Nationale Plantentuin van België, Domein van Bouchout, B-1860 Meise, Belgium

[1]Katholieke Universiteit Leuven, Instituut voor Plantkunde, Laboratorium voor Plantensystematiek, Kard. Mercierlaan 92, B-3001 Heverlee, Belgium

[2]Instituto de Investigação Cientifíca Tropical, Centro de Botánica, Trav. Conde da Ribeira 9, P-1300 Lisbon, Portugal

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Oxyanthus gossweileri from Angola has been described from a single specimen collected in 1906. A search in herbaria holding Angolan collections has revealed an additional flowering specimen, allowing a sound morphological and pollen morphological investigation. It is concluded that *O. gossweileri* must be kept in the Gardenieae – Gardeniinae but deserves generic segregation. A new genus *Ganguelia* is described and the necessary new combination made. *G. gossweileri* is a pyrrhophytic geofrutex with densely hairy, suborbicular leaf blades with subpalmate venation. Chorologically, *Ganguelia* is endemic in the western part of the Zambezian Region; in the Rubiaceae, the monospecific *Calanda* (Knoxieae) has a very similar narrow distribution. *Ganguelia* seems to exhibit two pollen morphological features which are not yet observed among the Gardenieae genera with tetrad pollen, namely, the ± acalymmate condition of the tetrads and the colpoidorate grains. However, these latter occur together with the pororate ones characteristic for Gardenieae tetrads. A part of the tetrads are decussate; this arrangment, not yet reported from the Rubiaceae, was previously overlooked in several genera and is hence not a peculiarity of the new genus.

Keywords: Acalymnate pollen tetrads, decussate pollen tetrads, *Ganguelia* gen. nov., *Gardenia*, *Oxyanthus gossweileri*, pollen morphology, pyrrhophytic geofrutex, Rubiaceae – Gardenieae.

*To whom correspondence should be addressed

Introduction

In a recent investigation of the genus *Oxyanthus* (Sonké 1990), supervised by one of us (E.R.), the species *Oxyanthus gossweileri* from Angola was excluded and its position left doubtful, mainly because the type examined was too poor for an in-depth examination. A search in herbaria holding Angolan collections (COI, LISC, LISJC, LISU and ZT) has revealed one additional flowering specimen in two sheets. Although fruits are still not available, a reinvestigation of this remarkable species is now possible and is presented here.

Material and Methods

Only one herbarium specimen was traced, in addition to the type, as a result of the above-mentioned search (*Teixeira et al. 8903*, see Taxonomy for whereabouts). This specimen was used for the dissection of one mature flower bud.

A small quantity of pollen, removed from a single flower, was available and for the sake of security, a preliminary preparation was made by embedding some grains in Hoyer's medium. The proper pollen sample was acetolysed according to Reitsma (1969) and observed by both light and scanning electron microscopy (S.E.M. Jeol 6400, 15 kV). Broken grains were obtained by shaking the pollen suspension in the presence of glass beads (Huysmans *et al.* 1994). Because orbicules have recently been found to be rather common in Rubiaceae (Huysmans *et al.* 1995), one open anther was additionally critical-point dried to observe unacetolysed pollen and to check the possible presence of orbicules on the interior anther wall. Most of the pollen in the dried anther was removed using a fine cactus needle and pollen measurements were made on S.E. micrographs of acetolysed grains. Palynological terminology follows Punt *et al.* (1994), whereas morphological terms are after Robbrecht (1988).

Observations

Habit and structure

O. gossweileri is a geofrutex having massive woody underground parts and tender supraterranean twigs (Figure 1A). These are hardly branched and very congested, reaching less than 10 cm in length.

Vegetative parts. Leaves (Figure 1B) are densely hairy and have suborbicular blades borne on slender petioles 1.5–2 cm long. Blades have a ± emarginate apex (the midvein often terminating in a small mucro) and a widely cuneate base. Blades are coriaceous to almost succulent. Their mesophyll has many idioblasts filled with tannins (these are also abundant in other organs) and others filled with crystal sand.

Leaf venation is as unusual for Rubiaceae as is the above-described shape, namely that the lateral nerves tend to arise from the blade bases (subpalmate).

Stipules are interpetiolar, ovate with acute tip. They are free to the base (not sheathing at all).

Fertile region. Flowers are solitary and probably first terminal, later pushed in a pseudo-axillary position; they are subtended by ovate bracteoles with acute tip.

The flowers (Figure 1D) are pentamerous and have left-contorted aestivation. The *calyx* (Figure 1E, H) is long-tubular and provided with narrowly triangular lobes. The *corolla* consists of a slender tube 4–5 cm long, crowned by narrow lobes of about 2 cm in length.

There are five *anthers* (Fig. 1F) sessile in the uppermost part of the corolla tube, their point of attachment situated at $^1/_3$ from their base. Their connective protrudes in a small apical triangular sterile appendage.

The united *style* in mature bud slightly surpasses the anthers, which are sessile just below the throat. It is almost thread-like, but its upper part is slightly swollen; it terminates in two short, papillar *stigmatic arms* (Figure 1G). An annular disk surrounds the base of the style.

The *ovary* is two-locular with axile placentation; the two peltate, slightly elongated placentas are adnate to ± the entire septum. Each placenta bears about 15 ovules. *Fruits* are unknown.

Indumentum and colleters. Almost all parts of the plant, vege-

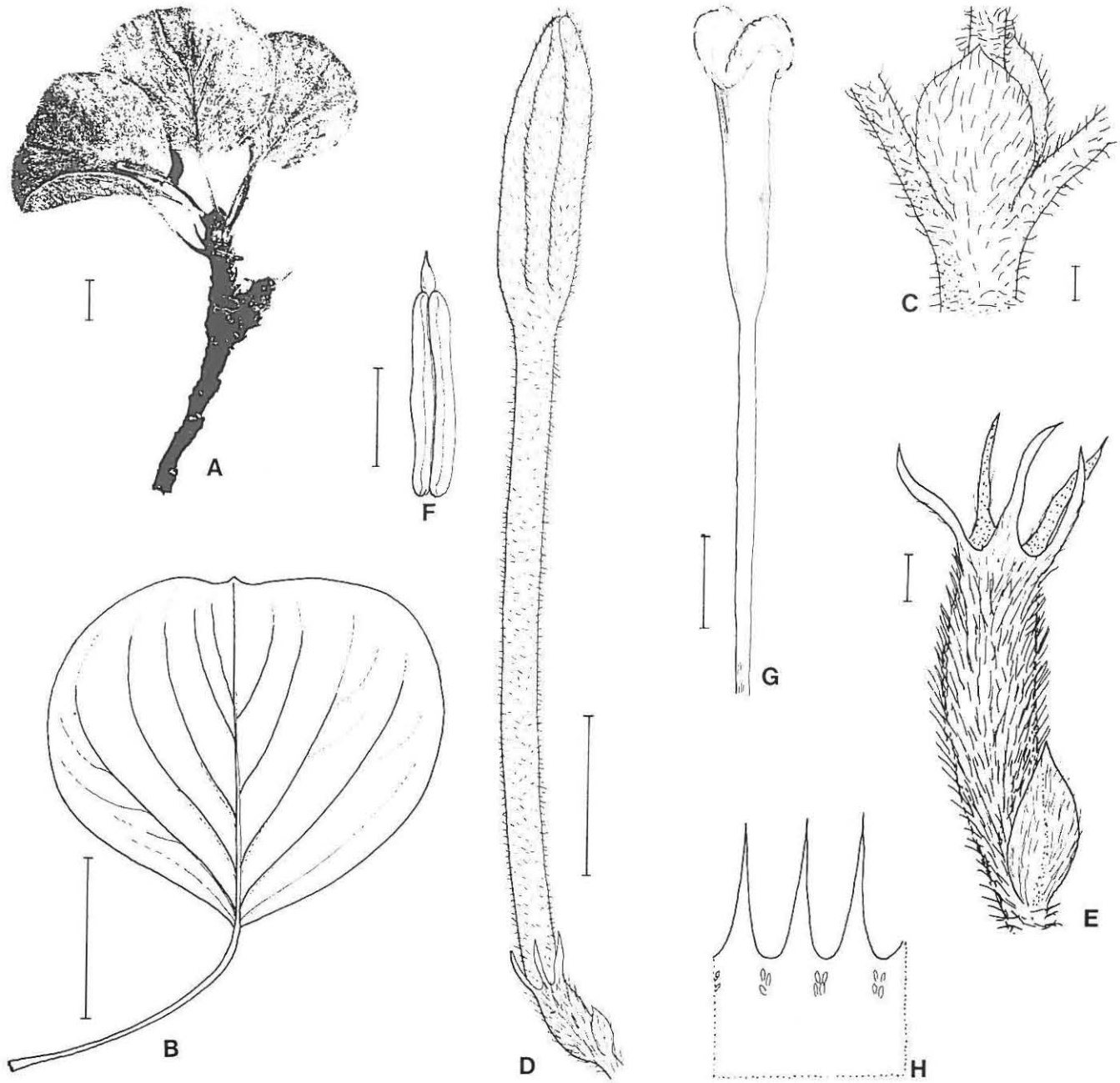

Figure 1 *Ganguelia gossweileri*. (A) Xerograph of vegetative aerial stem; (B) schematic representation of shape and venation of a leaf (hairiness not drawn); (C) node showing stipules; (D) mature flower bud; (E) bracteole, ovary and calyx; (F) anther; (G) apical part of style, showing swollen upper part and short stigmatic arms; (H) schematic representation of colleter position inside the calyx. Illustrated from *Teixeira et al. 8903* (COI). Scale lines = 1 cm (A, B, D) or 1 mm (all others).

tative as well as fertile, are densely covered with long soft hairs. Stipule insides, however, are glabrous, except for a basal row of hairs intermingled with colleters. Bracteoles have silky hairs and no colleters inside.

Inside the calyx, there are small groups of 3–5 colleters below each sinus between the lobes. Hairs are pluricellular and belong to the cylindrical type.

Pollen. The pollen grains are united in permanent tetrads, being tetrahedral (± 70%; Figure 2A, B) or decussate (± 30%; Figure 2C); a single rhomboidal uniplanar tetrad has also been observed. The size of the decussate tetrads is slightly larger (60–66 µm) than the more common tetrahedrally shaped tetrads (53–60 µm). The individual grains measure ± 34 µm. The tetrads are slightly acalymmate: fusion of the individual grains is moderate, and a suture line, caused by differences in the structure of the tectum, is visible between them (Figure 2B). The tectum, hence, forms a continuous envelope around the unit, but is more loose in between the monads. Internally (proximally), the exine is extremely thin (Figure 2H); our broken grains do not permit the observation of more details (transmission electron microscope studies would be needed for better understanding).

Individual grains vary from mostly 3-pororate (Figure 2F) to occasionally more or less 3-colpoidorate (Figure 2E). In the latter case, colpi are very short with rounded ends. Apparently the transition from colpoidorate to pororate is explainable by reduction of the ectocolpi until they are congruent with the endopori. The apertures meet two by two at six points on the tetrad (Fischer's law). The diameter of the ectoporus (in pororate grains) varies from 4.5 to 5.7 µm. Colpoidorate grains show a short ectocolpus with irregular edges and a granular colpus mem-

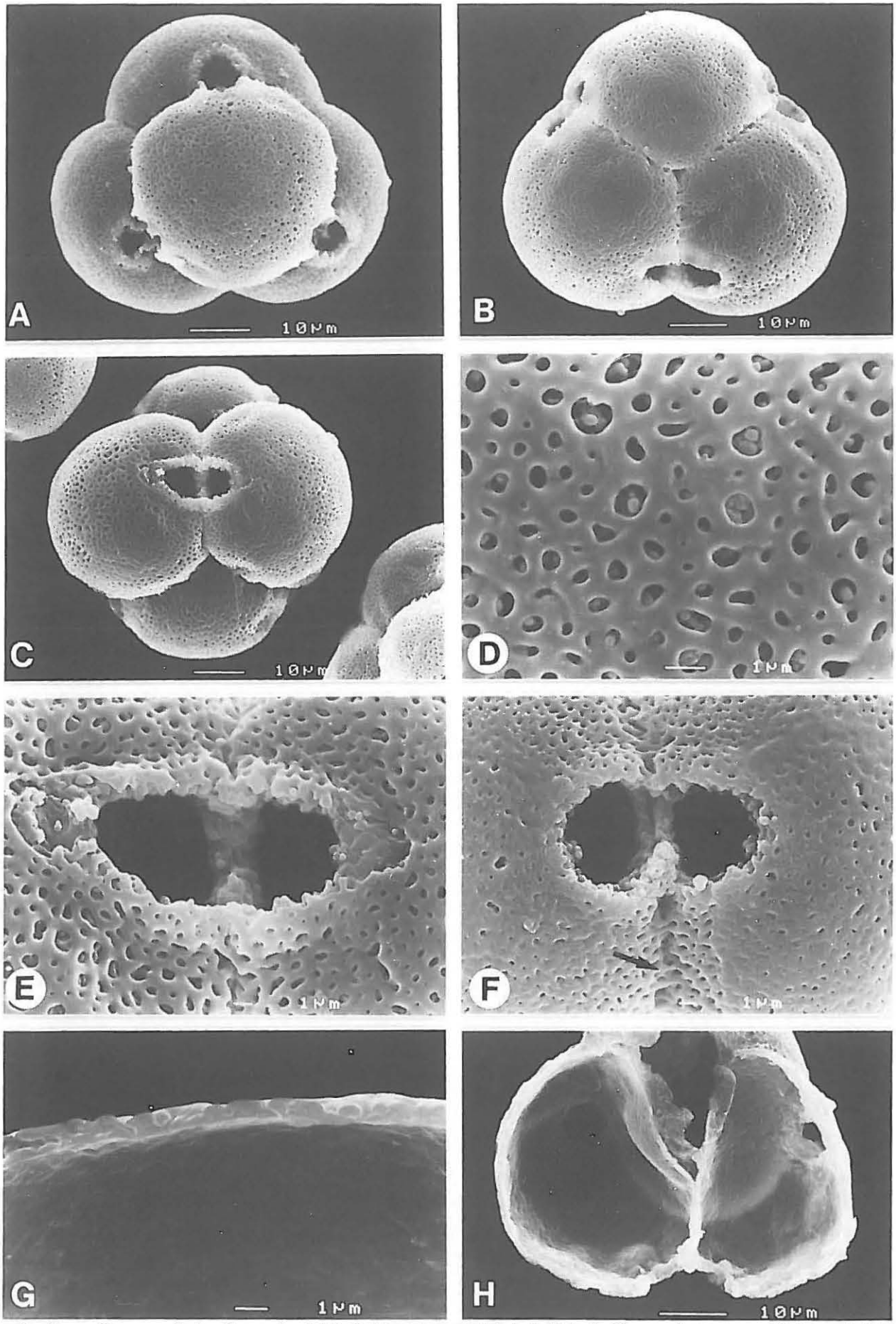

Figure 2 *Ganguelia gossweileri*, pollen grains. (A) & (B) Two views of a tetrahedral tetrad with opposite apertures; (C) decussate tetrad; (D) detail of perforate to microfoveolate sexine on pole of top grain in A; note granules on nexine in puncta; (E) & (F), two extremes of variation in apertures, colpoidorate in E, pororate in F; (G) cross section of thin pollen wall on pole, without columellae; (H) broken tetrad showing homogeneous inside of two grains.

brane. The endoporus (Figure 2H) has a faint costa which is only slightly protruding.

The smooth tectum is perforate to microfoveolate, with granules on the nexine in the puncta (Figure 2D); it is supported by very short columellae. Near the apertures and on the distal poles, the tectum is microfoveolate, i.e. the columellae are almost completely or completely lacking (Figure 2G). The rounded perforations are up to 1 µm in diameter (= puncta). On the nexine, small granules or free-standing bacula are often visible in the puncta. There are no supratectal processes. The exine is very thin (< 1 µm); the thickness of the sexine is equal or slightly larger than that of the nexine. The endexine is homogeneous and bumpy; no granules occur.

No orbicules have been observed on the inner anther wall.

Floral biology. Hardly any information is available, and only fully mature flower buds (just before anthesis) were collected. The anthers in these buds were observed to have opened and released part of their pollen. It adheres to the swollen upper part of the style lying between the anthers. Proterandry and secondary pollen presentation consequently seem to be present. The very long and narrow floral tubes combined with the presence of a disk suggest sphingid pollination.

Ecology

O. gossweileri is, according to its known geographic distribution, restricted to White's (1983) mapping unit 47, which is a mosaic of *Brachystegia bakerana* thicket and edaphic grassland.

The species is probably pyrrhophytic or, at least, fire tolerant, as indicated by the woody underground parts and the signs of burning present in the two examined specimens. Pyrrhophytes and geofrutices are common in the grasslands of the central plateau, where fires are frequent, and usually flower before the end of the dry season.

O. gossweileri occurs on sandy soils, forming groups with 1–2 m diameter, and produces flowers simultaneously with the production of leaves on new shoots in September and October, i.e. at the end of the dry season.

Distribution

The species is apparently endemic to a narrow part of south-central Angola (districts Bié and Cuando-Cubango). The two examined specimens were collected in the central African Plateau, at about 300 km from one another. *Gossweiler* 3275 was collected on the left margin of the Quiriri river, near Cassuango, i.e. in the eastern part of the region sometimes designated as the Ganguelas (Diniz 1973). The locality (known as Cassoango) is shown on Gossweiler's Carta fitogeográfica de Angola (1939) near Longa (district Cuando-Cubango). However, recent maps do not mention this locality and no information on its location could be obtained from the local populations during an expedition to this area in 1960 (E.J. Mendes, unpublished data included in the card catalogue of Angolan localities for internal use at LISC). The more recent specimen *Teixeira et al. 8903* was collected further north, between Cuemba and Munhango (district Bié).

Discussion

The generic position of *O. gossweileri*

S. Moore originally assigned the species to *Oxyanthus*, without proper comment on its generic position ('a very remarkable plant on account of its lowly habit and small leaves'). His choice was surely based on floral ressemblances.

There is ample evidence to place this documented remarkable Angolan species in the same tribe as *Oxyanthus*, namely, the Gardenieae. The large flowers in pseudo-axillary position, contorted aestivation, and multi-ovulate placentas make a position in this tribe obvious, despite the absence of fruits, which have high value for tribal diagnosis in the Ixoroideae. Our finding that the pollen grains are in permanent tetrads corroborates this, and excludes the Gardenieae – Diplosporinae.

In Rubiaceae, tetrad pollen is very rare. It is restricted to one of the three genera of the Henriquezieae (a neotropical tribe needing no further consideration here), and to 13 of the more than 60 genera of the Gardenieae – Gardeniinae. In this subtribe, tetrads occur especially in the African representatives, and characterize the 11 following African genera: *Preussiodora, Pleiocoryne, Oligocodon, Calochone, Massularia, Macrosphyra, Atractogyne, Oxyanthus, Mitriostigma, Euclinia* and *Gardenia*. Tetrads are not known from tropical Asian Gardeniinae; in the New World, they are restricted to *Casasia* and *Randia* (Robbrecht & Puff 1986, Table 1).

With the exception of *Gardenia*, and including the genus *Oxyanthus* to which the species was assigned, the 11 African Gardeniinae genera with tetrad pollen mentioned above are typical rain-forest genera showing a multitude of morphological differences with *O. gossweileri*. *Oxyanthus*, the genus to which the species was originally assigned, should be ruled out, in particular because of the habit (in *Oxyanthus* only trees and large shrubs, except for one species being a monocaul dwarf shrub), inflorescences (many-flowered in *Oxyanthus*), leaf-morphology (in *Oxyanthus* large ± elliptic leaves having relatively short petioles and penninerved acuminate blades up to 70 cm long), the anthers (in *Oxyanthus* generally a well-developed connective having apical and basal sterile appendages) and the style (in *Oxyanthus* the stigmatic lobes above the swollen style apex are minute and non-diverging). In addition, *Oxyanthus* is an essentially Guineo–Congolian and Afromontane forest genus.

Only *Gardenia* contains a large number of species which are well adapted to Sudano–Zambezian conditions, among them even three geofrutescent species, *G. subacaulis* (widely distributed in the eastern part of the Zambezian region), *G. brachythamnus* (Zambezian region: Botswana and Zambia) and *G. tinneae* (a species of the eastern part of the Sudanian region, known from the Central African Republic, Chad and Sudan). *G. subacaulis* and *G. tinneae* are clearly assignable to *Gardenia*, notably subgenus *Bergkias* (Verdcourt 1979). The latter author even considered *G. subacaulis* so closely related to *G. ternifolia* that 'the specimens [of *G. subacaulis*] are certainly not just variants of *G. ternifolia* due directly to burning.' It is obvious that *O. gossweileri* is definitely not a member of *Bergkias* having characteristic, more stout flowers with short tubes, wide lobes and exserted anthers.

There are two reasons which make a further comparison of *Gardenia* with *O. gossweileri* difficult, (1) the unknown fruits of the latter, and (2) the lacunar knowledge of the relationships within the rather heterogeneous genus *Gardenia*. The narrow corolla tubes of *O. gossweileri* do exist in African representatives of *Gardenia*, notably *G. vogelii* and *G. leopoldiana*, however its highly derived leaf morphology makes it impossible to consider these two species as candidate relatives. A morphological illustration of *G. leopoldiana* (Robbrecht & Pauwels 1993, Figure 191) shows several detail differences, such as the distribution of colleters over the whole surface of the base of the calyx tubes. More importantly, the above-mentioned geofrutescent *Gardenia brachythamnus* also has narrow corollas. This former *Randia* has first been related to *Xeromphis* (= *Catunaregam*) by Keay (1958) and was later transferred to *Gardenia* (Launert 1960). This geofrutex is a rather tall, branched shrub with decumbent to ± erect stems from long rhizomes. Its miniature, coriaceous leaves are tufted on short shoots which also bear the terminal, solitary flowers. *G. brachythamnus* needs detailed morphological and anatomical investigation, but seems closely related to the African

Gardenias with small, leathery, few-seeded fruits, such as *G. fiorii*.

Finally and most importantly, all species of *Gardenia* have parietal placentation. It is not very likely that it should have shifted to axile placentation in one single species, deviating in other important features. We consequently believe that *O. gossweileri* is neither an *Oxyanthus* nor a *Gardenia* and are convinced that it needs segregation in a new genus.

Chorological facts somewhat support this conclusion, although little is known about the degree of generic endemism of this part of Angola. White (1983: 87) stated that there are only a few endemic genera in the Zambezian region as a whole; he enumerated only six genera, all monospecific, but restricted his list to woody ones. In the Rubiaceae, in total 13 genera (woody and herbaceous ones) were found to be endemic of the Zambezian region (Robbrecht, unpublished). Only one of them, the equally monospecific *Calanda* (tribe Knoxieae, distribution map in Puff & Robbrecht 1989), is restricted to Angola; it has a generic distribution pattern fully comparable to that of the genus recognized here. It should be stressed that the area where the two geofrutescent taxa *Calanda* and *O.gossweileri* occur is the most important diversity centre for this growth form in tropical Africa (White 1976). In Africa, the Rubiaceae seem to be the family containing the largest number of geofrutices; this life form has evolved independently many times and in nine different tribes (Robbrecht 1988: 36).

A last question remains to be answered: is the separate generic status supported by pollen morphological characteristics?

Persson (1993) gave a general palynological overview of the subtribe Gardeniinae. His generic descriptions are concise, but many genera are illustrated by S.E. micrographs. Pollen of the Gardeniinae from Gabon was studied by Keddam-Malplanche (1985). The two genera discussed above, *Oxyanthus* and *Gardenia*, are thus documented palynologically.

Keddam-Malplanche (1985: 42) discussed the pollen morphology of nine representatives of *Oxyanthus* from Gabon. *O. gossweileri* fits into the general description of the genus, save for the thickness of the exine, varying between 1.75 and 5 µm in *Oxyanthus*, while in this case it never exceeded 1 µm.

Pollen of *Oxyanthus speciosus* was depicted by Robbrecht & Puff (1986: 104) and Persson (1993: 575). The sexine ornamentation slightly deviates from *O. gossweileri*, the given measurements, however, fit well. The latter author carefully mentioned the occurrence of colpoidorate grains ('porus ends rounded to slightly acute').

Persson's (1993: 570) generic description of *Gardenia*, based on the observations of only two species (*G. augusta* and *G. spathulifolia*) out of *ca.* 120, matches quite well with *O. gossweileri*: the '3-porate' tetrads (tetrahedral in his pictures; in our opinion 3-pororate) have also an exine thinner than 1 µm. The size of the tetrads, however, is smaller: 45–46 µm against 53–66 µm in *O. gossweileri*.

As regards the other African Gardeniinae genera with tetrads, descriptions and/or illustrations are available for all genera (Robbrecht 1978: *Preussiodora*; Persson 1993). They all have 3-por(or)ate grains but most of these genera deviate from the species we studied in having a reticulate sexine with sometimes a decreasing lumina size towards the poles (*Atractogyne, Calochone, Euclinia, Macrosphyra*, and *Preussiodora*). *Oligocodon* and *Mitriostigma* pollen also differ conspiciously from *O. gossweileri* in sexine ornamentation: the former genus has perforate pollen beset with spines and verrucae, pollen of the latter is rugulate with branched columellae. Only the description of *Pleiocoryne* pollen (no illustrations) resembles the studied species in a few important characters: perforate sexine with no columellae, a very thin exine (0.4 µm), and 'a granulate membrane near the ora.' This lianescent genus from West and Central Africa was documented by Kirkbride & Robbrecht (1984); it shows numerous morphological differences with the species discussed here, however, for example in the many-flowered inflorescences.

Decussate tetrads have not explicitly been reported from the Rubiaceae. Keddam-Malplanche (1985) did depict tetrahedral and decussate tetrads on her S.E. micrographs of *Oxyanthus*, and only decussate tetrads on her illustrations of *Gardenia*, but she did not mention at all the occurrence of these two types of tetrads. Persson (1993) illustrated only tetrahedral tetrads but made no mention of the arrangment in his descriptions. We infer that decussate tetrads were previously overlooked in rubiaceous literature but are relatively rare; they are at present reported from *Oxyanthus, Gardenia* and our new genus.

On the whole, the tetrad-possessing Gardeniinae are rather stenopalynous and not studied well enough to make a more sound comparison with *O. gossweileri* possible. It nevertheless seems that we have detected the following two characteristics not yet observed in other genera of the subtribe and consequently possibly supporting the separate generic status: (1) the tetrads being slightly acalymmate, and (2) colpoidorate grains occurring together with pororate ones.

Taxonomy

***Ganguelia** Robbr.* gen. nov.

Geofrutex verisimiler pyrrhophyticus propter flores pseudo-axillares, corollae aestivationem contortam, placentas multiovulatas et granos pollinis in tetradis dispositos nullo dubio Gardeniis (subtribu Gardeniinis) pertinet ubi genus *Gardenia* aliquot similis placentatione axile autem differt.

Generic name after the Ganguelas, region of Angola where the type specimen was collected.

***Ganguelia gossweileri** (S. Moore) Robbr.* comb. nov.

Oxyanthus gossweileri S. Moore, Journal of Botany 49: 151 (1911).

Bié district: Cuemba – Munhango, 35 km [*ca.* 12°12' S, 18°35' E], 28 Sept. 1965, *Teixeira et al. 8903* (COI, LISC).

Cuando-Cubango district: Cassuango, Quiriri River [*ca.* 14°39' S, 18°40' E], 18 Oct. 1906, *Gossweiler 3275* (holotype BM; iso. in COI not seen).

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